Overstory influences on light attenuation patterns and understory plant community diversity and composition in southern boreal forests of Quebec

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Abstract: We have characterized overstory light transmission, understory light levels, and plant communities in mixedwood boreal forests of northwestern Quebec with the objective of understanding how overstory light transmission interacts with composition and time since disturbance to influence the diversity and composition of understory vegetation, and, in turn, the further attenuation of light to the forest floor by the understory. Overstory light transmission differed among three forest types (aspen, mixed deciduous–conifer, and old cedar-dominated), with old forests having higher proportions of high light levels than aspen and mixed forests, which were characterized by intermediate light levels. The composition of the understory plant communities in old forests showed the weakest correlation to overstory light transmission, although those forests had the largest range of light transmission. The strongest correlation between characteristics of overstory light transmission and understory communities was found in aspen forests. Species diversity indices were consistently higher in aspen forests but showed weak relationships with overstory light transmission. Light attenuation by the understory vegetation and total height of the understory vegetation were strongly and positively related to overstory light transmission but not forest type. Therefore, light transmission through the overstory influenced the structure and function of understory plants more than their diversity and composition. This is likely due to the strong effect of the upper understory layers, which tend to homogenize light levels at the forest floor regardless of forest type. The understory plant community acts as a filter, thereby reducing light levels at the forest floor to uniformly low levels.

Résumé : Nous avons caractérisé la transmission de la lumière par le couvert dominant, les niveaux de lumière en sous-étage et les communautés végétales dans les forêts boréales mixtes du nord-ouest du Québec. L'objectif de l'étude était de comprendre comment la transmission de la lumière par le couvert dominant interagit avec la composition et le temps écoulé depuis la dernière perturbation pour influencer la diversité et la composition de la végétation en sous-étage et, par la suite, l'atténuation supplémentaire de la lumière au sol causée par ce sous-étage. La transmission de la lumière par le couvert dominant était différente entre les trois types forestiers (peuplements dominés par le peuplier, par un mélange de conifères et de feuillus et par de vieux thuyas), les vieilles forêts ayant de plus fortes proportions de niveaux élevés de lumière que les forêts de peuplier et mixtes qui étaient caractérisées par des niveaux intermédiaires de lumière. La composition des communautés végétales du sous-étage des vieilles forêts était la plus faiblement corrélée à la transmission de la lumière par le couvert dominant, même si ces forêts montraient la plus grande variation de transmission de la lumière. La plus forte corrélation entre les caractéristiques de transmission de la lumière par le couvert dominant et les communautés végétales en sous-étage a été observée pour les forêts de peuplier. L'indice de diversité des espèces était généralement plus élevé dans les forêts de peuplier, mais était faiblement relié à la transmission de la lumière par le couvert dominant. L'atténuation de la lumière par la végétation du sous-étage et la hauteur totale de cette végétation étaient fortement et positivement reliées à la transmission de la lumière par le couvert dominant, mais pas au type forestier. Par conséquent, la transmission de la lumière par le couvert dominant a davantage influencé la structure et la fonction des plantes du sous-étage que leur diversité et leur composition. Ce résultat est probablement attribuable à l'effet prononcé de l'étage dominant qui tend à homogénéiser le niveau de lumière atteignant le sol peu importe le type forestier. Ainsi, la communauté végétale du sous-étage agit comme un filtre qui réduit les niveaux de lumière atteignant le sol à des niveaux uniformément faibles.

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Introduction

Understanding how light levels in the understory are influenced by both overstory and understory species is crucial for predicting boreal forest dynamics, since competition for light among understory herbs, shrubs, and trees may influence the rate and direction of succession. Although some studies have investigated the effect of understory vegetation as a competitive factor reducing light levels for regenerating trees in clearcuts (e.g., Knowe et al. 1996), there have been relatively few studies that have examined light attenuation by understory vegetation in boreal forests (but see Constabel and Lieffers 1996; Messier et al. 1998; Aubin et al. 2000). Even fewer studies have examined how light attenuation by boreal understory plants is related to a gradient of overstory light transmission. Because the percent cover of understory shrubs and herbs has been shown to be positively related to overstory light transmission (Klinka et al. 1996), it is expected that light attenuation by understory plants will be positively related to overstory light transmission. Whether or not light attenuation by the understory plants varies as a function of forest type has important implications for understanding the functional significance of the understory community.

The forest understories of the mixedwood boreal forests of Quebec are characterized by vigorous shrub and herb communities (Bergeron et al. 1983; De Grandpré et al. 1993; Légaré et al. 2001) that have been shown to greatly reduce light levels at the forest floor (Messier et al. 1998; Aubin et al. 2000). There is evidence that the early survival and growth of tree species are inhibited at the very low light levels within, and under, these dense understories (Parent et al. 2002). Therefore, the characterization of light attenuation by the understory plant community is critical for accurately modelling understory light levels and for understanding dynamics in these forests.

Of equal importance in our understanding of boreal forest dynamics is how strongly composition and diversity of vascular plant species are related to overstory variables, such as stand composition, age since disturbance and light transmission. Although age since disturbance has been shown to affect understory diversity and composition in closed boreal mixedwood forests (De Grandpré et al. 1993), overstory species composition was reported to have no effect on understory species diversity in the same forests (Légaré et al. 2001). In tropical forests, species partitioning into "light availability niches" in the understory is believed to be one of the processes contributing to patterns of species diversity and composition (Denslow 1987). In boreal forests, however, with very different disturbance and light regimes, the mechanisms controlling composition and diversity are not clear.

The work presented here was designed to address five key questions regarding the relationship between overstory and understory dynamics in mixedwood boreal forests of Quebec: (*i*) how does the distribution and availability of light in the understory differ among three dominant forest types; (*ii*) does overstory light transmission play a role in structuring understory plant communities; (*iii*) do overstory species composition and stand age (independent of light transmission) play a role in structuring understory plant communities; (*iv*) do overstory and understory canopies operate to homogenize light at the forest floor; and (*v*) what are the implications for boreal tree dynamics? To answer these questions, we compared the composition, diversity, and light-interception patterns of understory plant communities across a wide gradient of overstory light transmission in three dominant forest types. The gradient was determined by systematically measuring overstory light transmission at widely spaced intervals along random transects within each forest type. Instead of comparing understory response in gap and nongap microsites (the "Swiss cheese" approach, sensu Lieberman et al. 1989), we were able to examine the response of the understory across a gradient of light levels and characterize the understory light environment both accurately and without bias (Lieberman et al. 1989; Clark et al. 1996; Nicotra et al. 1999).

The plant community was examined at three levels of biological organization: the plant community as a whole, plant life forms, and species. Life form and species-level responses provided valuable information about life-history characteristics, environmental requirements, and interactions of all components of the community. These relationships between the availability of resources and plant life-history characteristics can be helpful in explaining the diversity and distribution of species in the forest understory (Nicotra et al. 1999).

Materials and methods

Study area and forest types

The study area encompasses a large area surrounding Lac Duparquet in the Abitibi region of northwestern Quebec, Canada, ranging from 48°15′ to 48°30′N and from 79°15′ to 79°30′W. This area experiences a cold and continental climate characterized by a mean annual temperature of 0.8 °C, an annual mean precipitation of 800–900 mm, and 64 frost-free days (Environment Canada 1993). The landscape is a flat to gently rolling lowland (150–300 m) situated in the southern portion of the Clay Belt, a large physiographic region characterized by glacio-lacustrine clay deposits. Soils were classified as grey luvisols (Agriculture Canada Expert Committee on Soil Survey 1978) and were compact and fine-textured with moderate to good drainage (Brais and Camiré 1992). High base cation content and well-structured surficial mineral horizons account for high productivity in these soils (Brais et al. 1995).

The study area is located in the southern limit of the boreal forest and has been classified as the Balsam fir – White birch (*Abies balsamea* (L.) Mill. – *Betula papyrifera* Marsh.) climax region of the Boreal Shield Ecozone (Bergeron et al. 1983). These forests are transitional between the black spruce (*Picea mariana* (Mill.) BSP) boreal forests to the north and the northern temperate hardwood forests to the south. Sample sites were selected in three dominant forest types which vary in structure, age, and species composition: (*i*) pure aspen forests, (*ii*) mixed deciduous–conifer forests, and (*iii*) old-growth cedar-dominated forests, hereafter referred to as "aspen," "mixed." and "old" forest types, respectively. Aspen forests were almost exclusively comprised of trembling aspen (*Populus tremuloides* Michx.), with very minor components of *Betula papyrifera*, white spruce (*Picea glauca* (Moench) Voss), and jack pine (*Pinus banksiana* Lamb.). Mixed forests had an average of 46% conifer component but were still dominated by aspen with various amounts

Table 1. Sampling information for each sampled forest stand.

Study sites	No. of plots	Transect distance (m)	Stand age (years)[a]	Overstory light transmission (% full sunlight)[b]	Conifer trees (%)[c]
Pure aspen					
1	40	1000	70–75	7.7–32.2	
2	23	575	65–70	8.8–27.2	
3	28	700	70–75	7.7–26.8	
4	17	425	55–60	11.8–22.2	
5	17	425	55–60	10.2–23.0	
6	20	500	50–55	9.2–40.3	
7	16	400	65–70	9.2–37.5	
8	14	350	65–70	9.6–21.4	
Total[d]	175	4375	50–75	7.7–40.3	
Mixed forests (>30% conifers)					
1	40	1000	75–80	2.9–65.8	48.9 (20.9–72.7)
2	30	750	75–80	9.5–36.6	44.2 (7.1–86)
Total	70	1775		2.9–65.8	46.1 (7.1–86)
Old forests					
1	40	1000	240	6.2–59.25	81.7 (50–97)
2	30	750	240	8.1–61.9	92.6 (72.7–100)
3	40	975	240	11.9–59.3	93.6 (71.4–100)
Total	110	2725		6.2–61.9	88.9 (50–100)

[a]Ages were determined from increment cores taken at 1.0 m height in summer of 2000.
[b]Overstory light transmission was calculated from hemispherical photographs of the forest canopy taken at 4 m (above the understory vegetation).
[c]The percentage of confir canopy trees was not quantified in aspen stands. Aspen stands were nearly or completely pure aspen.
[d]There were 39 additional plots sampled in aspen forests to increase the number of samples of high overstory light transmission (values ranged from 20.1 to 58.7% full sunlight).

of *Abies balsamea*, *Betula papyrifera*, *Picea glauca*, and *Picea mariana*. Old forests were dominated by eastern white cedar (*Thuja occidentalis* L.) accompanied by *Abies balsamea*, *Betula papyrifera*, and *Picea glauca*. Mixed and aspen forests have been considered as two different successional pathways that later succeed to old forests (Dansereau and Bergeron 1993). The aspen and mixed forests originated from fires between 1916 and 1944; and the old forests originated from a large fire in 1760 (Dansereau and Bergeron 1993; Table 1).

Fire is considered the major natural disturbance agent in the region (100 year fire return intervals), but small-scale gap disturbances are present in all forest types (Kneeshaw and Bergeron 1998). Canopy gaps in aspen forests are generally formed when single trees or small groups of trees die; in mixed and old forests where *Abies balsamea* is more abundant, larger gaps created by spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks are common (Kneeshaw and Bergeron 1998). Old forests have experienced numerous spruce budworm outbreaks (Bergeron et al. 1995).

Field sampling

To select similar mesic sites and reduce some variation due to edaphic conditions, we used ecosystem maps and classification methods developed by Bergeron et al. (1983) for the same study area; the classification system is based chiefly on soil deposit, soil drainage, and geomorphology. We selected sites on flat to gently sloped terrain, and we characterized soil type and texture to ensure that all our sites were on moderately to well-drained clay soils. In areas not studied by Bergeron et al. (1983), we used similar methods developed for nearby Ontario (Taylor et al. 2000) to find analogous site types. Sites with human-caused disturbances were carefully avoided, and edge influences were minimized by establishing transects at least 50 m from openings and roads. Forest stands ranged in size from 4 to 500 ha. Eight stands were selected in aspen forests, two stands in mixed forests, and three in old forests (Table 1). There were fewer replicate stands in old and mixed forests, because they were less common on the landscape and were in areas of high infestation of forest tent caterpillars (*Malacosoma disstria* Hbn.). A large outbreak of forest tent caterpillars severely defoliated *Populus tremuloides* and *Betula papyrifera* trees across the Abitibi region during sampling in 2000. We sampled all accessible mixed and old forest stands that were not affected by the outbreak.

Parallel transects were established at 25 m intervals in each sample stand. Transect distances per stand depended on the stand size, and were as long as possible up to a maximum of 1000 m per stand (Table 1). A total of 4375 m of transects was established in pure aspen forests; 1775 m, in mixed forests; and 2725 m, in old forests. Transects were randomly oriented in large stands; but in smaller stands, transects were laid out at orientations to maximize transect length.

Overstory light transmission

Hemispherical photographs were taken systematically under appropriate sky conditions every 25 m along each transect to

characterize light transmission through the overstory canopy. Sample points 25 m apart were considered to be independent samples and not spatially autocorrelated (Clark et al. 1996; Nicotra et al. 1999). We sampled at 175, 70, and 110 locations in aspen, mixed, and old forest types, respectively. Preliminary analysis showed that pure aspen forests had very few high-light environments (or large canopy gaps). Since one of the objectives of this study was to characterize understory vegetation and light attenuation patterns across a wide gradient of overstory light conditions, we sampled 37 additional plots in the sunniest positions of large gaps in five additional aspen stands.

A 35 mm camera with a Minolta 7.5mm/F4 true fish-eye lens was used to take all photographs. The camera was mounted in a self-levelling bracket, oriented north, attached to a telescoping pole and stabilized by a large tripod. Canopy photographs were taken at 4 m above the forest floor to represent light conditions affected by the overstory and not understory vegetation. When the understory was taller than 4 m (35% of all samples), it was pressed below the camera. This was supported by Canham et al. (1994) who found little difference between light levels measured between 1 and 7.5 m in the absence of understory vegetation.

We used the canopy photographs to calculate overstory light transmission using GLA version 2 software following Canham (1988) and Frazer et al. (2000). The analysis integrates the daily and seasonal distribution of solar radiation transmitted through the overstory into a single index of available light in units of percentage of full sunlight for a specified growing season (early May to early September).

Vegetation community

At each sample point along each transect, the maximum height and presence of each vascular plant species rooted in a 1 m^2 plot was recorded. A larger 4 m^2 plot was used to include taller understory species that were present at higher intervals but were not rooted in the 1 m^2 plot. Species identification followed Marie-Victorin (1995). Sampling took place from late June to mid-August 2000. The relative abundance of each species was visually estimated in five vertical intervals (layers): layer 1 (forest floor to 1 m); layer 2 (1–2 m); layer 3 (2–3 m); layer 4 (3–4 m); and layer 5 (greater than 4 m). All ocular estimates of relative abundance were performed by the same individual. Relative abundance was used as a measure of the compositional importance of a given species. Abundance of each species was estimated as a proportion of all plant material in the layer (e.g., if only one species was present, then it would represent 100%; if a species is not present, then 0%). Relative abundance estimation permitted the calculation of diversity indices and was considered more efficient and accurate than estimation of percent cover.

Vertical profile of light attenuation and availability

Light levels in units of photosynthetically active radiation (PAR; $\mu mol \cdot m^{-2} \cdot s^{-1}$) were measured at each canopy photo sample point at heights of 0, 1, 2, 3, and 4 m above the forest floor and 4 m with taller vegetation removed (where applicable). The line sensor provided an average of quantum measurements across its entire sensing area (12.7 mm wide × 1 m long) and was recommended for use within heterogeneous plant canopies (LI-COR, Inc. 1991; LI-COR, Lincoln, Neb.). The sensor was levelled prior to recording measurements. Four sets of measurements were taken at each height in four directions and averaged to give one mean value per height. All light measurements per plot were taken under similar sky conditions (the vast majority under completely overcast skies) and within a very short period of time to reduce variation due to changing sky conditions.

Percent transmission of light through the understory was calculated by dividing PAR measured at each height by PAR measured at 4 m (with taller vegetation removed if required). This was then multiplied by overstory light transmission (calculated from hemispherical photographs taken at the exact same location, in units of percent full sunlight). We define "light availability" as percentage of full sunlight reaching a given height in the understory and distinguish this from "overstory light transmission," which is the amount of light transmitted through the overstory to the top of the understory vegetation. Gendron et al. (1998) demonstrated that hemispherical photographs provide a good estimation of the mean seasonal light availability reaching any location in the understory. Furthermore, the same study demonstrated that one measure of PAR made at any time during the day under both sunny and overcast sky conditions using a point quantum sensor can be used to determine the mean seasonal light availability in the understory, although the relationship is better on overcast days. Here we used the mean of four 1 m long quantum sensor measurements to determine the mean seasonal light availability of each location, so that the reliability of our measurements should be even better.

Data analysis

All statistical analyses were performed using SYSTAT 6.0 (Wilkinson et al. 1996). Values were log transformed when necessary to homogenize the variance or satisfy assumptions of normality. Overstory light transmission was compared among forest types using a one-way analysis of variance (ANOVA). Bonferroni pairwise comparison tests were used to compare means. Frequency distributions of overstory light transmission were compared among forest types using Kolmogorov–Smirnov two-sample nonparametric tests. Supplemental high-light samples in aspen forests were not included in this analysis; therefore, the number of independent plots analysed was 166, 63, and 106 for aspen, mixed, and old forests, respectively. These numbers differed slightly from the total number sampled (Table 1) due to problems with photographic processing.

Richness, Shannon–Weaver diversity (H'), and evenness (J) indices of both species and life forms were calculated for each understory layer (Whittaker 1972). Species were grouped into six plant life forms: (*i*) graminoids (5 species); (*ii*) ferns and fern allies (i.e., including species of *Lycopodium* and *Equisetum*; 13 species); (*iii*) herbs (43 species); (4) deciduous shrubs (13 species); (*v*) conifer shrubs (1 species); and (*vi*) conifer saplings (4 species). Two species of deciduous saplings were also found, but they were not present in sufficient numbers to include in life form analyses

An analysis of covariance (ANCOVA) (using the general linear model procedure in SYSTAT; Wilkinson et al. 1996) was used to examine how forest type and overstory light transmission influence the diversity, evenness, and richness

of species and life forms; maximum height of the understory; total number of species per plot; as well as light attenuation and light levels at different heights (0–4 m) in the understory. Forest type was the factor, and light transmission by the overstory was the covariate. Each vertical interval was analysed separately for species and life form variables; plant diversity indices at heights greater than 4 m (layer 5) were not analysed because one species totally dominated (mountain maple, *Acer spicatum* Lam.). For all ANCOVAs (and multivariate analyses of covariance (MANCOVAs) used for other analyses) performed, the mean of the covariate was subtracted from the covariate to clarify the interpretation of the main effect in the ANCOVA (Wilkinson et al. 1996). All ANCOVA and MANCOVA models used the supplemental 39 high-light plots that were measured in the aspen forests.

The relative abundance of life forms and species were examined using a MANCOVA, which used the same model structure as the ANCOVA, but compared the mean relative abundances of each of the 6 plant life forms or each of 61 species simultaneously to evaluate the effect of forest type and overstory light transmission. The Pillai trace multivariate test statistic was used, because it is most robust to violations of MANCOVA assumptions (Wilkinson et al. 1996). Significant effects in the MANCOVAs were examined more closely using univariate F tests and multivariate analyses of variance (MANOVAs). Additionally, the relative abundance of each life form and species was regressed with overstory light transmission within each forest type, and differences among forest types were analysed using a one-way ANOVA

Nonlinear regression in the form of the Michaelis–Menten equation ($Y = (a \times \text{light})/(a/s + \text{light}) + \epsilon$) was used to relate light attenuation at the forest floor to overstory light transmission for each forest type. The distribution of understory light availability and attenuation levels at each height was compared among forest types using Kolmogorov–Smirnov two-sample tests (not including supplemental high-light plots in aspen forests). One-way ANOVAs were performed to compare average light availability and light attenuation patterns among the forest types at different heights in the understory.

Results

Overstory light transmission

Average overstory light transmission was higher in old forests (27% full sunlight) than in aspen and mixed forests, which did not differ (18–19% full sunlight) (ANOVA, $p < 0.001$). In contrast, frequency distributions of overstory light transmission were significantly different in each forest type ($p < 0.05$, Kolmogorov–Smirnov tests). Light levels less than 10% full sunlight were rare in all forest types (5%, 8%, and 3% of measurements in aspen, mixed, and old forests, respectively) and only one measurement was less than 5% full sunlight. Old forests generally had a wider range of light levels with approximately one-third of the measurements greater than 30% full sunlight (Fig. 1). Aspen and mixed forests had a high proportion of light levels between 10 and 20% full sunlight and only 1% and 8% of light measurements, respectively, were greater than 30% full sunlight (Fig. 1).

Fig. 1. Frequency distributions of overstory light transmission in aspen, mixed, and old forests. Bars are 5% increments of full sunlight.

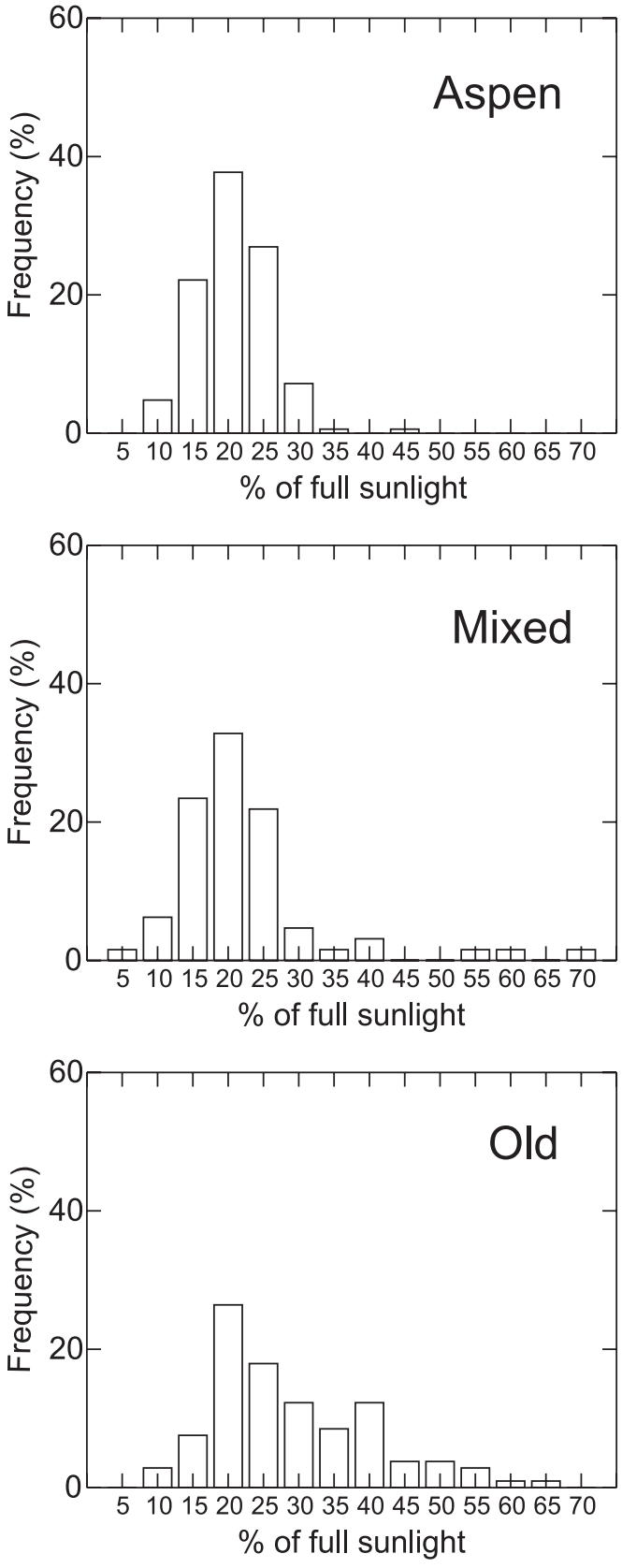


Table 2. Maximum height and total number of understory species per plot as a function of overstory light transmission and forest type.

	Forest type		Overstory light transmission		Forest × overstory light transmission	
	F	*p*	*F*	*p*	*F*	*p*
Total number of species per plot	77.897	<0.001	3.102	0.079	2.724	0.067
Maximum height of understory	1.312	0.27	50.635	<0.001	3.548	0.03

Note: Values are *F* statistics and *p* values from an analysis of covariance with forest type as the factor and overstory light transmission as the covariate.

Understory community structure and composition

The total number of species in a plot was more strongly related to forest type than to overstory light transmission whereas the opposite was true for the height of the understory, although there was an interaction between forest type and light (Table 2). The understory plant community was composed of significantly fewer species in old forests ($7/m^2$) than mixed ($10.6/m^2$) and aspen ($10.8/m^2$) forests, which did not differ ($p < 0.05$, Tukey's means separation test). The height of the understory community ranged from 39 to 850 cm and was remarkably similar (means ranged from 340 to 347 cm) among the three forest types (ANOVA, $p = 0.95$; Kolmogorov–Smirnov tests, $p > 0.05$). Understory height was positively and significantly related to overstory light transmission in aspen and mixed forests (linear regression; $r^2 = 0.24$ and 0.15, respectively, $p < 0.001$) but not in old forests. In contrast, species numbers were positively related to forest light transmission in old forests only ($p = 0.029$).

The diversity patterns illustrated in Fig. 2 show that forest type had a greater influence on species diversity than on life form diversity. There were few differences in form diversity patterns among forest types, particularly in higher layers (Fig. 2, Table 3*a*), whereas differences in patterns of species diversity were evident in all but a few layers (Table 3*b*). Nevertheless, old forests had generally higher life form diversity and evenness than the other forest types in layer 2, and aspen forests had higher life form evenness and lower life form richness than old and mixed forests in layer 1 (Fig. 2). In all layers, old forests supported a less diverse array of species per plot compared with mixed and aspen forests (Fig. 2). Because herb species were generally more abundant in aspen and mixed forests than in old forests, differences in layer 1 were largely due to the lower number of herb species in old forests. Likewise, differences in taller layers may be attributed to a higher diversity of deciduous shrubs in aspen and mixed versus old forests.

In contrast to forest type, differences in overstory light transmission had little influence on species diversity patterns (Table 3*b*). Species diversity and evenness in layer 1 were influenced by overstory light transmission but not at higher layers (Table 3*b*). In contrast, life form richness in all layers and life form diversity in layer 1 were strongly related to overstory light transmission, whereas life form evenness was only weakly related (Table 3*a*).

The composition of plant life forms in layer 1 (0–1 m) was strongly influenced by forest type and overstory light transmission (Table 4). The relative abundances of all six life forms differed among forest types (univariate *F* tests, $p < 0.05$). Old forests had more conifer shrubs (Canada yew, *Taxus canadensis* Marsh.) and conifer saplings and fewer herbs, ferns, and deciduous shrubs than mixed and aspen forests in layer 1 (Fig. 3).

Deciduous shrubs dominated higher layers of the understory in all forest types (Fig. 3). The mean abundances of life forms differed among the three forest types in layers 2 and 3 but were similar in layer 4 (Table 4). Overall, old forests had lower relative abundances of deciduous shrubs and higher abundances of conifer saplings and conifer shrubs compared to aspen and mixed forests (Fig. 3).

In layer 1, overstory light transmission influenced the relative abundances of deciduous shrubs, herbs, ferns, and graminoids, whereas conifer shrubs and saplings were not affected (Table 4). The significant interaction in the MANCOVA ($p = 0.009$; Table 4) can be attributed to the overriding response of life forms to canopy light transmission in aspen forests ($p < 0.001$) compared with other forest types ($p > 0.05$). In aspen forests, high overstory light transmission favoured graminoids, ferns, and deciduous shrubs, whereas herbs were favoured at low overstory light transmission.

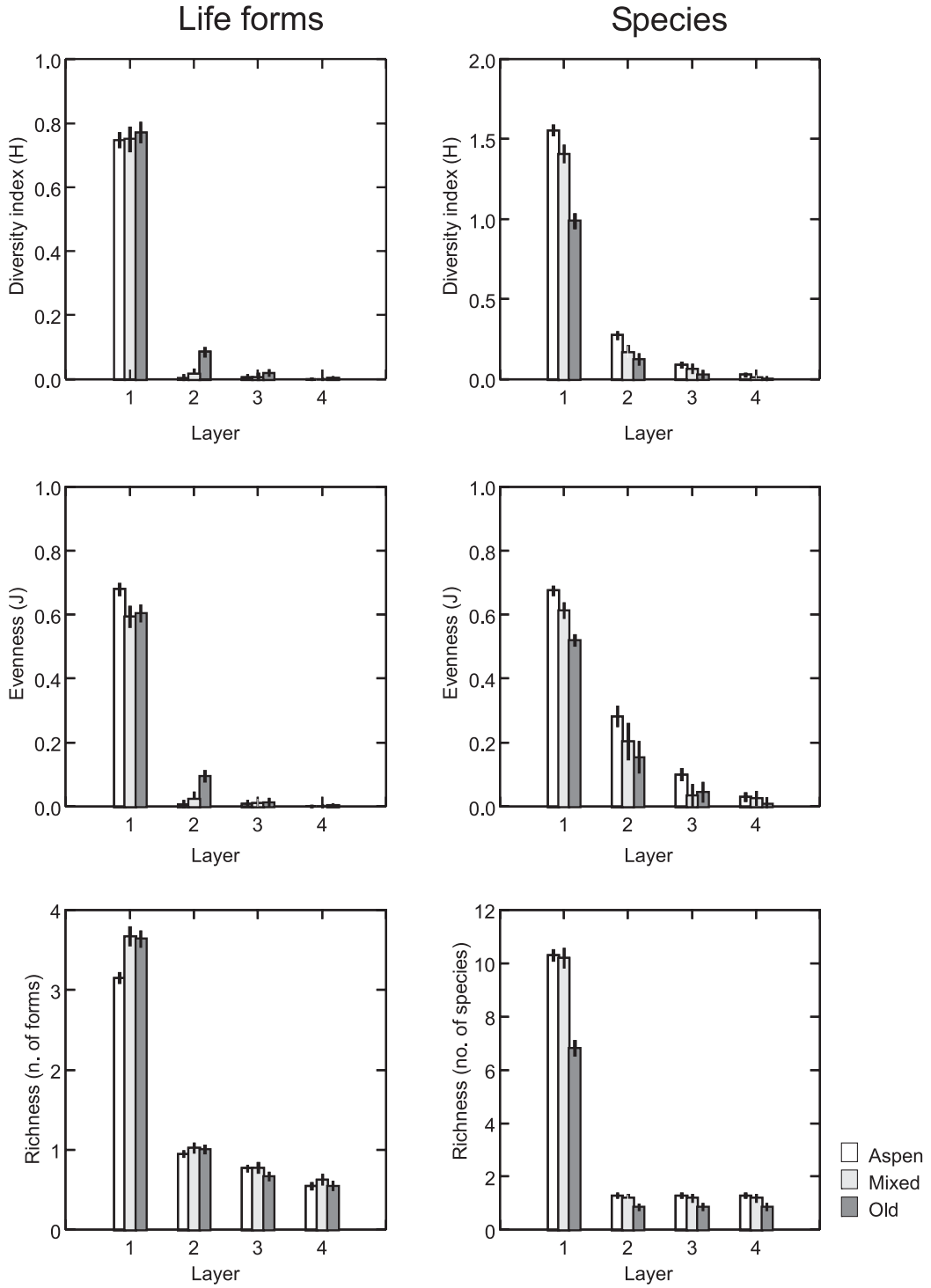
The effect of overstory light transmission on life form composition was also significant for taller understory layers (layers 2–4; Table 4). The relative abundance of deciduous shrubs was significantly related to overstory light transmission in aspen and mixed forests in layers 3 and 4; in layer 2, no significant relationships were observed (linear regression, $p > 0.05$).

Plant species distributions

In all layers of the understory, plant species composition was influenced by both forest type and overstory light transmission (MANCOVA, $p < 0.001$). One-way ANOVAs showed that only 21 of the species had relative abundances that differed among forest types in layer 1 ($p < 0.05$). Evergreen species such as *Taxus canadensis*, *Abies balsamea*, *Thuja occidentalis*, and low-lying herbs such as *Coptis groenlandica*, *Mitella nuda*, and *Linnaea borealis* had higher relative abundances in old forests. Higher relative abundances of *Equisetum sylvaticum* and *Athyrium felix-femina* occurred in mixed forests and of *Galium triflorum*, *Rubus idaeus*, and *Streptopus roseus* occurred in aspen forests. *Aralia nudicaulis*, *Aster macrophyllus*, *Corylus cornuta*, and species of *Carex* were associated with both aspen and mixed forests and less so with old forests.

Species relative abundances in layer 1 of old forests were not correlated with overstory light transmission (MANOVA, $p = 0.352$). In mixed forests, five species had significant relationships with overstory light transmission: *Impatiens capensis*, *Ribes lacustre*, *Rubus idaeus*, *Trientalis borealis*, and *Viola* spp. increased relative abundance with increased light transmission. In aspen forests, *Alnus rugosa*, *Circaea alpina*, *Dryopteris spinulosa*, *Galium triflorum*, *Impatiens*

Fig. 2. The diversity (*H′*), evenness (*J*), and richness of plant life forms and species in four understory layers and three forest types.



capensis, *Rubus idaeus*, *Equisetum sylvaticum*, *Ribes glandulosum*, *Cinna latifolia*, and species of *Viola* were positively related to light transmission, whereas *Aralia nudicaulis*, *Diervilla lonicera*, *Maianthemum canadensis*, and *Aster macrophyllus* were negatively related.

Differences among forest types in layer 2 were mostly due to *Abies balsamea*, *Acer spicatum*, *Taxus canadensis*, and *Alnus rugosa*; whereas differences in response to light transmission were attributed to *Alnus rugosa*, *Abies balsamea*, and *Rubus idaeus*, which increased in relative abundance with increased overstory light transmission, and *Corylus cornuta*, which decreased. In layers 3 and 4, *Alnus rugosa* increased with increased light transmission in aspen forests ($p < 0.001$). *Acer spicatum* was more abundant in mixed and old forests and *Alnus rugosa* more abundant in aspen forests.

Light attenuation by the understory

Light attenuation and light levels in the understory were affected more strongly by overstory light transmission than by forest type (Table 5). In fact, there were no differences in

Table 3. (A) Plant life form and (B) plant species diversity, evenness and richness as a function of forest type and overstory light transmission.

(A) Plant life form diversity, evenness, and richness.

	Forest type		Overstory light transmission		Forest × overstory light transmission	
	F	*p*	*F*	*p*	*F*	*p*
Layer 1						
Shannon-Weaver (*H′*)	0.251	0.778	12.351	<0.001	0.23	0.795
Evenness (*J*)	5.108	0.006	0.645	0.422	0.495	0.61
Richness (no. of forms)	15.708	<0.001	11.818	0.001	0.216	0.806
Layer 2						
Shannon-Weaver (*H′*)	16.592	<0.001	3.73	0.067	2.403	0.092
Evenness (*J*)	0.724	0.486	4.215	0.041	3.234	0.04
Richness (no. of forms)	1.381	0.252	10.524	0.001	2.046	0.131
Layer 3						
Shannon-Weaver (*H′*)	0.941	0.391	0.225	0.636	0.118	0.889
Evenness (*J*)	0.184	0.832	0.432	0.512	0.261	0.77
Richness (no. of forms)	0.182	0.833	23.649	<0.001	0.499	0.608
Layer 4						
Shannon-Weaver (*H′*)	1.647	0.194	0.324	0.569	0.321	0.726
Evenness (*J*)	0.717	0.489	0.311	0.578	0.328	0.721
Richness (no. of forms)	5.615	0.004	23.367	<0.001	6.514	0.002

(B) Plant species diversity, evenness, and richness.

	Forest type		Overstory light transmission		Forest × overstory light transmission	
	F	*p*	*F*	*p*	*F*	*p*
Layer 1						
Shannon–Weaver (*H′*)	67.747	<0.001	4.723	0.03	0.934	0.394
Evenness (*J*)	31.044	<0.001	5.839	0.016	0.616	0.541
Richness (no. of species)	62.452	<0.001	0.662	0.416	2.116	0.122
Layer 2						
Shannon–Weaver (*H′*)	9.606	<0.001	0.824	0.365	1.152	0.317
Evenness (*J*)	3.161	0.044	0.026	0.871	2.536	0.081
Richness (no. of species)	7.542	0.001	2.857	0.092	0.131	0.877
Layer 3						
Shannon–Weaver (*H′*)	3.482	0.032	2.345	0.127	0.497	0.609
Evenness (*J*)	2.298	0.102	0.011	0.915	0.356	0.7
Richness (no. of species)	7.064	0.001	3.236	0.073	0.073	0.802
Layer 4						
Shannon–Weaver (*H′*)	2.099	0.124	0.454	0.501	3.262	0.039
Evenness (*J*)	0.613	0.542	0	0.993	1.77	0.172
Richness (no. of species)	7.064	0.001	3.236	0.073	0.221	0.802

Note: Values are *F* statistics and *p* values from an analysis of covariance with forest type as the factor and overstory light transmission as the covariate.

understory light attenuation or light availability among forest types at any height in the understory, except for light level at 0 m (Table 5). In contrast, overstory light transmission strongly influenced light attenuation levels and light availability at all heights in the understory (Table 5). Light levels at the forest floor showed the weakest relationship ($p = 0.029$) to overstory light transmission. Linear regression revealed that this relationship was not significant in aspen ($p = 0.163$) and old forests ($p = 0.931$). This suggests that understory plant communities in these two forest types acted as differential filters, attenuating light to the same levels irrespective of overstory light transmission.

Understory light attenuation (i.e., from the top of the understory to the forest floor) was extremely variable (ranged from 10 to 90%) at low overstory light transmission as evidenced by the broad scatter below 20% full sunlight and was higher (>80%) and less variable at higher overstory light transmission (Fig. 4). Because of this variability at low overstory light transmission, nonlinear regression models explained only 15 to 17% of the variation at the forest floor ($p < 0.001$). At 1–4 m heights in the understory of all forest types, there was considerable variability in light attenuation across the gradient of overstory light transmission.

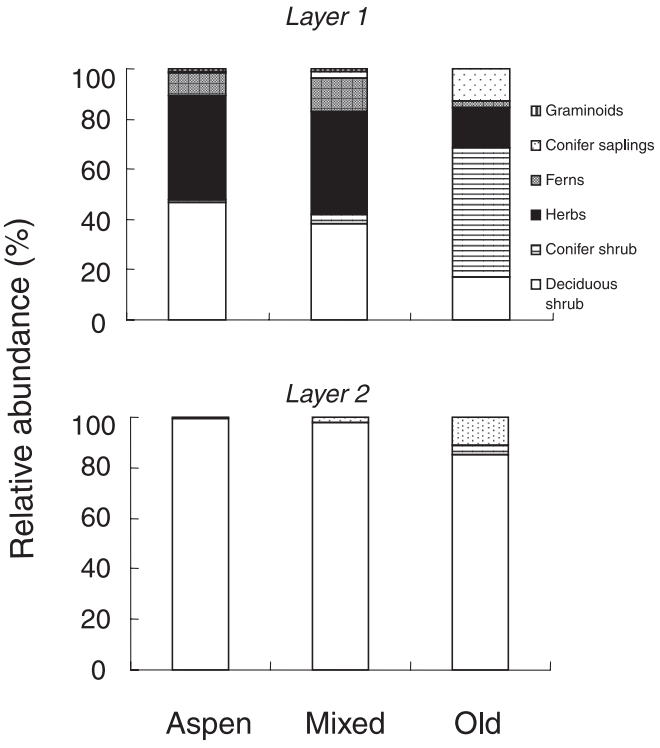
In general, most light attenuation occurred between the forest floor and 1m height, but high levels of light attenuation were also observed between 3 and 4 m under more open

Table 4. Relative abundance of plant life forms as a function of overstory light transmission and forest type.

	Forest type		Overstory light transmission		Forest type × overstory light transmission	
	F	*p*	*F*	*p*	*F*	*p*
Layer 1						
Model (Pillai trace)	35.393	<0.001	5.965	<0.001	2.231	0.009
Deciduous shrubs	55.518	<0.001	8.531	0.004	6.129	0.002
Conifer shrubs	277.188	<0.001	0	0.999	0.177	0.838
Herbs	42.055	<0.001	22.024	<0.001	5.776	0.003
Conifer saplings	23.033	<0.001	0.1	0.752	2.939	0.054
Ferns	12.447	<0.001	6.71	0.01	0.693	0.501
Graminoids	8.61	<0.001	10.186	0.002	2.48	0.085
Layer 2						
Model (Pillai trace)	7.262	<0.001	7.703	<0.001	3.086	0.005
Deciduous shrubs	18.984	<0.001	3.314	0.069	0.96	0.384
Conifer shrubs	4.13	0.017	3.838	0.051	4.049	0.018
Conifer saplings	8.555	<0.001	5.507	0.019	4.31	0.014
Layer 3						
Model (Pillai trace)	2.647	<0.001	12.155	<0.001	1.032	0.390
Deciduous shrubs	3.986	0.019	21.466	<0.001	1.191	0.305
Conifer saplings	2.014	0.135	1.203	0.273	1.134	0.323
Layer 4						
Model (Pillai trace)	0.424	0.792	12.39	<0.001	3.136	0.014
Deciduous shrubs	0.722	0.487	24.669	<0.001	6.009	0.003
Conifer saplings	0.068	0.934	0.021	0.885	0.108	0.898

Note: Values are *F* statistics and *p* values from multivariate analysis of covariance.

Fig. 3. Differences among forest types in the relative abundance of plant life forms in layers 1 and 2 of the understory.



forest canopies (Fig. 5). Distributions of light attenuation levels were very similar among forest types ($p > 0.20$) except at the forest floor, where mixed and old had slightly different distributions ($p = 0.038$), and at 4 m, where all forest types differed ($p \leq 0.028$). Resulting light levels at the forest floor were very low (means varied from 4.1 to 4.6% full sunlight), and the distributions did not differ among forest types ($p > 0.07$; Fig. 5). There were greater differences in frequency distributions of light levels from 2 to 4 m in the understory among forest types ($p < 0.013$; Fig. 5). However, at 1 m, aspen and mixed forests had similar distributions of light levels ($p = 0.522$) while old forests had a higher proportion of higher light levels.

Discussion

Understory light availability in southern boreal forests

Overstory light transmission in the southern boreal forests of our study region was both higher and more variable than in tropical and southern temperate forests (Chazdon and Fetcher 1984; Canham et al. 1990, 1994; Brown and Parker 1994; Clark et al. 1996), where canopy transmission was uniformly low (producing understory light levels <5% full sunlight). Average overstory light transmission was similar to that reported in Alberta for aspen-dominated boreal forests (Ross et al. 1986; Constabel and Lieffers 1996) and to northern temperate and boreal forests in British Columbia (Bartemucci et al. 2002) but was higher than pure spruce forests in Alberta (Lieffers and Stadt 1994) and closed canopy forests in the same study area (Messier et al. 1998).

We found that light levels characteristic of closed canopies (as reported in Messier et al. 1998) were rare at the stand level in all three forest types, suggesting that differences among forest types in our study were largely due to the level of small-scale gap disturbance. This was supported by a canopy gap study in the same forests, which found that old forests had 41% of their area in canopy gaps because of

Table 5. Light attenuation and light availability at five heights in the understory as a function of forest type and overstory light transmission.

Understory	Forest type		Overstory light transmission		Forest type × overstory light transmission	
height (m)	*F*	*p*	*F*	*p*	*F*	*p*
Percent attenuation						
0	1.490	0.227	40.898	<0.001	2.878	0.057
1	2.041	0.130	19.263	<0.001	1.337	0.264
2	1.239	0.377	15.766	<0.001	0.848	0.429
3	1.857	0.158	11.744	0.001	4.109	0.017
4	2.599	0.076	18.443	<0.001	0.543	0.581
Light level (% full sunlight)						
0	3.101	0.046	4.786	0.029	4.616	0.010
1	2.475	0.086	35.275	<0.001	1.072	0.343
2	1.224	0.295	72.09	<0.001	1.079	0.341
3	1.622	0.199	162.771	<0.001	3.846	0.022
4	0.392	0.676	480.913	<0.001	1.593	0.205

Note: Values are *F* statistics and *p* values from an analysis of covariance with forest type as the factor and overstory light transmission as the covariate.

repeated spruce budworm outbreaks, whereas aspen and mixed forests usually had much less area in gaps (7–11%; Kneeshaw and Bergeron 1998). Although average overstory light transmission was similar in aspen and mixed forests, there were a few microsites of higher forest canopy light transmission in mixed versus aspen mature forests that may be critical for the persistence of shade-intolerant overstory and understory species later in succession. These differences emphasize the importance of comparing frequency distributions versus average light levels. Nicotra et al. (1999) demonstrated that similarities in average resource conditions (light) among forests can obscure biologically important variability and that an understanding of temporal and spatial patterning of resource availability may lead to a better understanding of regeneration processes.

Despite differences in stand-level distributions of overstory light transmission among forests, average light levels at the forest floor (approximately 4–5% full sunlight) were remarkably similar among forest types. Constabel and Lieffers (1996) also found no differences in light levels at the forest floor (approximately 6% full sunlight) among three forest types in northern Alberta. Our results suggest that despite great differences among forest types in understory species composition (and in overstory light transmission), there was relatively little difference in their capacity for light harvesting (Constabel and Lieffers 1996). The understory plant community can be seen as a differential filter reducing light levels at the forest floor to uniformly low light levels (Hill and Silander 2001). It is worth noting that light levels at the forest floor in our study were still higher than typical overstory light transmission in temperate and tropical forests.

Overstory light transmission and understory plant structure and function

Our results demonstrated that overstory light transmission played an important role in determining the cover and function of the understory plant community but had less of an influence on the composition and diversity of the species that make up that community. The most striking result was that light attenuation by the understory plant community was strongly influenced by overstory light transmission; however, forest type, which differed greatly in composition, in age since disturbance, and presumably, in soil properties, had little effect. That light attenuation patterns did not differ among forests highlights the strong functional significance of the understory plant community. Light attenuation patterns and other key results, such as total height, that were consistent across different forest types are essential to better understand the effect of understory dynamics on forest succession.

Because the composition of the understory has been shown to influence patterns of light attenuation (Messier et al. 1998; Aubin et al. 2000), we had expected that light attenuation patterns would vary among forest types. Old forests had very different understory plant communities than aspen and mixed forest types, but the average percentage of light attenuated was virtually the same in each forest type. Furthermore, the way in which the plant communities attenuated light across the gradient of overstory light transmission was remarkably similar among forest types. However, light attenuation by the entire understory plant community was extremely variable under closed forest canopies (i.e., low overstory light transmission) but was much higher and more predictable in large canopy openings (i.e., high rates of canopy transmission). This suggests that, at low overstory transmission, the understory plant cover is less predictable (more variable), whereas the understory plant cover is consistently dense at high overstory transmission. The vertical structure of light attenuation was also similar among forest types. Most understory light attenuation occurred between the forest floor and 1m, although there was also a trend for high light attenuation between 3 and 4 m, particularly at high overstory light transmission. Nevertheless, at higher heights in the understory, the variability in light attenuation levels was much higher across the

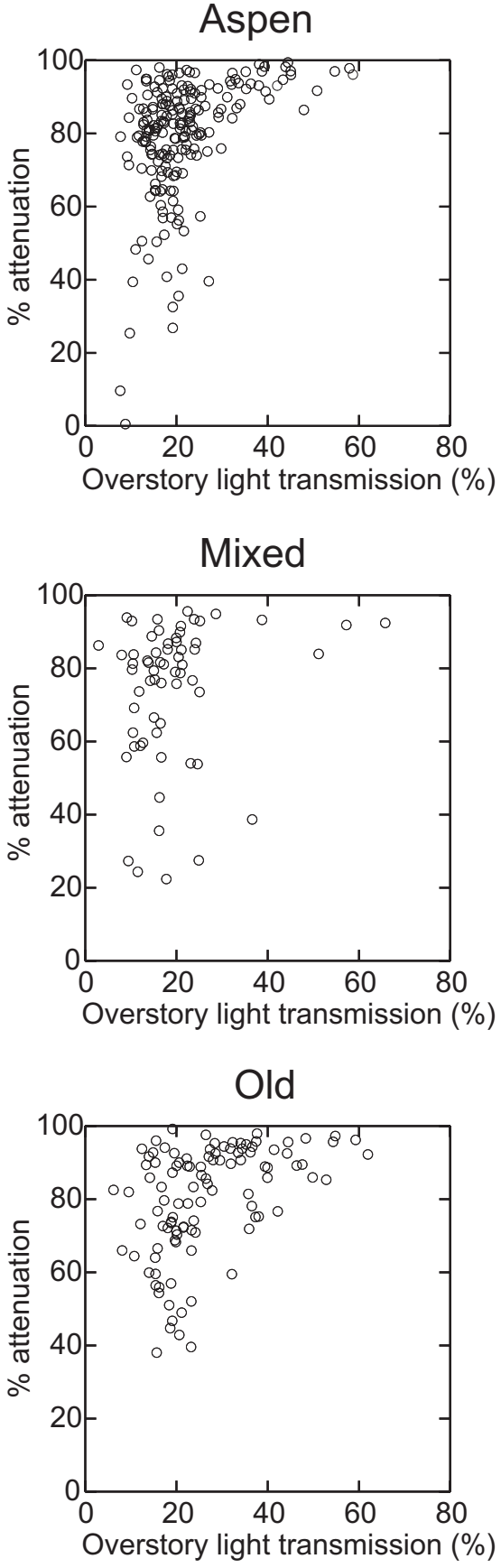


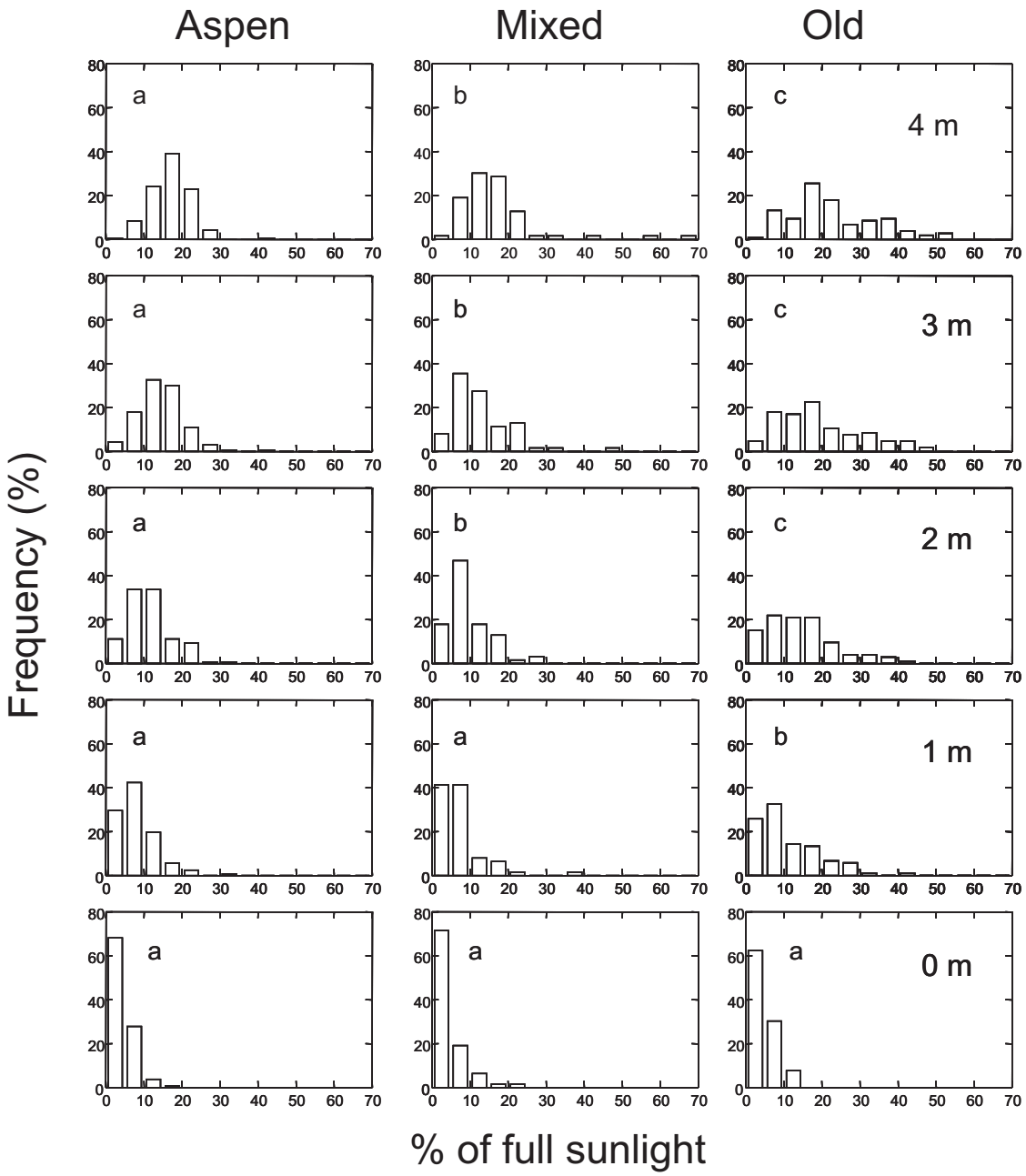
Fig. 4. Understory light attenuation (from the top of the understory vegetation to the forest floor) as a function of overstory light transmission and forest type.

gradient of overstory conditions. A constantly dense cover below 1 m was consistent with other studies (Messier et al. 1998; Aubin et al. 2000; Bauhus et al. 2001), and Aubin et al. (2000) reported high light attenuation at 3–4 m by dense *Acer spicatum* canopies.

Understory composition and structure

Predicting understory plant diversity and composition is a difficult task (Gilliam and Roberts 2003), and our results confirmed this. Although both life form diversity and composition were somewhat related to overstory light transmission, relationships were weak and never consistent among the forest types. Species composition and diversity, however, were highly variable and mostly unrelated to overstory light transmission, particularly in old forests, which may be due to the homogenizing effects of the upper understory layers. However, of the approximately 100 vascular plant species found in different understory layers, very few (18) showed affinities for high or low light availability, suggesting rather that most species have broad ecological amplitude for light. There was however a group of early successional species (e.g., *Rubus idaeus* and *Impatiens capensis*) in aspen and mixed forests that showed an affinity (although weak) for high levels of overstory light transmission. There were also species that seemed to show a competitive advantage at low levels of overstory light transmission (sensu Halpern and Spies 1995). *Aralia nudicaulis*, for example, was able to maintain higher relative abundance at low versus high understory light levels, which may suggest that it was shaded by vigorous deciduous shrub communities at higher light levels (e.g., *Acer spicatum*). Mixed forests had far fewer species associated with high or low light availability, which may be attributed to a paucity of high-light plots sampled in this forest type and the confounding factor of conifer composition. Within mixed forests, there was a gradient of conifer composition from pure aspen to mostly conifer (Table 1). We found that low-lying evergreen herbs such as *Coptis groenlandica*, *Linnaea borealis*, and *Cornus canadensis*, which are susceptible to smothering by deciduous litter (Whitney and Foster 1988), were associated with both low light levels and conifer canopies. The lack of change in composition and diversity in old forests across a range of overstory conditions was most surprising. Canopy gaps in old forests were found to have more productive forest floor and soil properties than the surrounding forest (Paré and Bergeron 1996), so we expected a higher diversity of species (or a change in species composition) in gaps compared with closed canopies. However, there was no change in species diversity or composition in areas of high overstory light transmission. Differences in mechanisms of gap creation among forest types may explain why understories in old forests showed the weakest response to overstory light levels. Gaps in aspen and mixed forests were usually created suddenly by the snapping of large *Populus tremuloides* boles (Kneeshaw and Bergeron 1998), which released resources quickly, whereas the death of *Abies balsamea* from spruce budworm attacks in old forests was slow and gradual.

Fig. 5. The frequency distribution of light levels in the understory from the forest floor to 4 m. Different letters within a row of graphs represent significant differences among forest types (Kolmogorov–Smirnov tests, $p < 0.05$).



Overall, we found little evidence that light limitation and niche partitioning of light resources by species was strong enough to explain diversity and composition patterns in any of the forest types (Denslow 1987; Svenning 2000). Instead, our results support those of Klinka et al. (1996) who proposed that, while overstory light attenuation affects the cover of the understory plant community, other factors such as forest stand composition and age, disturbance history, predisturbance composition, and the availability of propagules are more important in determining composition and diversity (e.g., Hubbell and Foster 1986). Of those studies that have specifically examined overstory light transmission influences on plant diversity, weak relationships were found for species richness of woody seedlings in tropical wet forests of Costa Rica (Nicotra et al. 1999) and for understory diversity in *Eucalyptus* forests in Australia (Bauhus et al. 2001).

The weak correlations between overstory light transmission and understory species composition and diversity found in our study and others may be due to inherent limitations in examining species occurrences data and light availability measured at one point in time. It is necessary to assess mortality and growth dynamics in response to temporal changes in understory light availability to fully understand light gradient partitioning in these forests (Kobe 1999). This may

be especially true for boreal species, which have unique regeneration strategies. Most understory species (approximately 70%) in these forests have the capacity to resprout from underground structures or germinate from seedbanks after fire and persist through succession via clonal growth (De Grandpré et al. 1993). Therefore, the species composition of the present community can be a function of establishment opportunities in the past (Hubbell and Foster 1986; De Grandpré et al. 1993), showing little response to current light conditions through persistence mechanisms such as large underground reserves. In fact, individuals of some of the long-lived perennial understory species might be older than many of the overstory trees (Ahlgren 1960). The weak relationships with overstory light transmission may also be attributed to the dominance of *Acer spicatum* in these forests. This shade-adapted shrub is able to respond rapidly to changes in light availability, making it abundant across a wide gradient of overstory conditions (Aubin 1999) and homogenizing understory light levels.

We found that forest type had a considerably stronger influence on indices of species diversity, perhaps through the effects of canopy composition and stand age on soil nutrient availability, pH and forest floor properties (Whitney and Foster 1988; Paré et al. 1993; Paré and Bergeron 1996). For example, Légaré et al. (2001) found that nutrient availability and soil properties were slightly better (e.g., higher pH and exchangeable Ca) under deciduous versus coniferous tree species in our study area. These differences, however, were not strong enough to result in higher understory diversity under deciduous overstories (Légaré et al. 2001). Although our study was not robust enough to separate the interacting effects of overstory composition and age, this does suggest that stand age may have the strongest influence on species diversity.

Understanding understory influences on canopy tree dynamics

The predictability of the understory plant structure and function in relation to differences in overstory light transmission is an important result of this study and will provide a foundation for incorporating understory plant dynamics into forest succession models. Although most forest models do not include understory light attenuation, it is evident that the understory plant community in these forests had a dramatic effect on light availability at a range of heights within the understory. Indeed, the rarity of high light levels from the forest floor to 1 m may profoundly influence canopy tree regeneration and secondary succession in these boreal forests as has been shown by George and Bazzaz (2003) in other deciduous temperate forests. The uniformly low light levels would favour the survival and growth of shade-tolerant tree species, such as *Abies balsamea*, which could grow slowly, experiencing many years of suppression before surpassing the understory layer (Parent et al. 2002). Clonal tree species (e.g., *Populus tremuloides*) able to benefit from parental connections might be able to rapidly grow through the understory vegetation, although aspen can only grow quickly enough to outcompete the understory vegetation in large gaps (Kelly et al. 1999). The change in light availability as the sapling grows through the understory layers also has important implications. One could expect to see higher growth rates as saplings surpass the dense 0–1 m layer and reach taller layers that are patchier, with more frequent high-light microsites (Constabel and Lieffers 1996; Lieffers and Stadt 1994). Juvenile survival may depend on whether the gains in growth rates due to higher light availability outweigh the increased costs of being a taller sapling (Claveau et al. 2002).

Incorporation of our results into models of forest dynamics could illustrate the role that the understory plant community plays in forest succession through its impact on growth and survival of tree seedlings and saplings (Pacala et al. 1996). A very simple approach to predicting light availability in the understory would be to attenuate light in these forests using the frequency distributions of light attenuation levels obtained in this study. The light attenuation levels derived for each height in the understory would act as filters to modify the overstory light transmission between 4 m and the forest floor. Using the frequency distributions will enable us to understand how the variability, as well as the average light attenuation levels, influences tree dynamics in the understory.

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